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Review Article

Lionfish (*Pterois miles*) in the Mediterranean Sea: a review of the available knowledge with an update on the invasion front

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Abstract

Invasive species often severely impact ecosystems and human activities in the areas that they invade. The lionfishes *Pterois miles* and *P. volitans* are regarded as the most successful invasive fishes in marine ecosystems. In the last 40 years, these Indo-Pacific predators have established in the tropical western Atlantic Ocean, with well-documented detrimental effects on the local fish communities. Around 10 years ago, a second invasion began in the Mediterranean Sea, which is being colonised by *P. miles*. Given the invasive potential of *P. miles* and the fact that the ecology and biodiversity of the temperate/sub-tropical Mediterranean Sea offer a different setting from the tropical western Atlantic, specific knowledge on this second invasion is needed. Here, we: (i) review the scientific knowledge available on the ecology of invasive lionfishes, (ii) discuss such knowledge in the context of invasion ecology and (iii) suggest future research avenues on the *P. miles* invasion in the Mediterranean Sea. In addition, we offer an update on the spread of *P. miles* in the Mediterranean Sea. While the history and development of the Mediterranean invasion are resolved and some mitigation plans have been implemented locally, the study of the interactions of *P. miles* with Mediterranean species and their impact on the local biodiversity is in its infancy. Closing this gap will lead to important fundamental insights in invasion ecology and will result in predictions on the impact of *P. miles* on the ecology and ecosystem services of the Mediterranean Sea. Such information will have practical implications for policy-makers aiming to devise sound and efficient mitigation plans.

Key words: Citizen science, exotic predators, invasion ecology, marine ecology, predation ecology

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Introduction

Invasive species are species that establish and spread in a new range at a high rate (Ricciardi 2013), often with detrimental effects on the local ecosystems. Invasive species can cause environmental degradation (Anderson and Rosemond 2007; Ehrenfeld 2010; Villamagna and Murphy 2010), carry and spread parasites (Gozlan et al. 2005; Iglesias et al. 2015) and compete for resources with native species (Bergstrom and Mensinger 2009; Polo-Cavia et al. 2010). Amongst the most severe ecological problems associated with biological invasions is biodiversity loss through local extinction of native species. This is particularly relevant when there is a direct trophic interaction between invader and local species. For example,

invasive mammalian predators caused the extinction of more than 100 species worldwide (Doherty et al. 2016) and the invasion of Lake Victoria by the Nile perch (*Lates niloticus*) drove almost 200 endemic cichlids to extinction (Witte et al. 1992). Due to their dramatic ecological impacts, invasive species are regarded as one of the most serious environmental problems of our time (Ricciardi 2013).

The lionfishes *Pterois miles* and *P. volitans* (hereafter, referred together as 'lionfish') are virtually undistinguishable and show almost identical morphological traits (Kulbicki et al. 2012). They are considered the most invasive fishes in the marine realm; native to the Indo-Pacific Ocean and Red Sea, lionfish reached the western Atlantic Ocean through intentional or accidental releases by aquarists (Kulbicki et al. 2012; Côté and Smith 2018). Lionfish were first detected in Atlantic waters in 1985 and became a common sight at certain locations in the late 1990s (Whitfield et al. 2002; Schofield 2009). Despite considerable control efforts at the local scale (de León et al. 2013; Dahl et al. 2016; Harris et al. 2019, 2020; Goodbody-Gringley et al. 2023), lionfish have spread through the entire tropical western Atlantic and continue to expand their invasive range along the Brazilian coast (Côté and Smith 2018; Soares et al. 2022, 2023). Lionfish are generalist predators (Green et al. 2011, 2014; Green and Côté 2014; D'Agostino et al. 2020) and are having an impact on the ecosystems of the western Atlantic by preying extensively on various local benthic and demersal fishes, including endemics of high conservation value (Albins and Hixon 2008; Green et al. 2012, 2014; Benkwitt 2015; Rocha et al. 2015; Ingeman 2016). Predation by lionfish can reduce recruitment of juveniles and the biomass of local species by up to 65% (Albins and Hixon 2008; Green et al. 2012). Such marked effects on the local biodiversity have been associated with impacts on the stability of coral reef ecosystems and their degradation (Lesser and Slattery 2011). More recently, a second lionfish invasion has begun in the Mediterranean Sea (hereafter, Mediterranean), which is being colonised by *P. miles* (Kletou et al. 2016; Bariche et al. 2017; Phillips and Kotrschal 2021). This second invasion raises concerns on possible impacts on the biodiversity and ecosystem services of the Mediterranean (Kletou et al. 2016; Savva et al. 2020).

The Mediterranean is a unique ecosystem: it is the largest enclosed sea on Earth and a highly biodiverse basin, home to more than 11000 animal species, some of which are found nowhere else in the world (Coll et al. 2010; Psomadakis et al. 2012). For example, of the approximately 540 native species of Mediterranean fishes, around 9% are endemic (Psomadakis et al. 2012). In addition, the sea provides economically valuable services to approximately 150 million people in the numerous countries on its coasts (Coll et al. 2010). At the same time, the Mediterranean is suffering from many anthropogenic stressors (Bianchi and Morri 2000; Coll et al. 2010) and it is the most invaded sea in the world. This is largely due to the opening of the Suez Canal (Edelist et al. 2013), which was constructed in 1869 to connect the Mediterranean with the Red Sea for commercial purposes (Costello et al. 2021). Initially, there was little scope for invasions due to the small size of the Canal and the presence of bitter lakes creating a hypersaline barrier between the two seas. However, the Suez Canal has been widened multiple times in recent years, increasing its capacity to carry propagules and reducing the salinity of the bitter lakes (Edelist et al. 2013; Galil et al. 2017; Castellanos-Galindo et al. 2020). New species ('Lessepsian species') enter the Mediterranean every year and the Suez Canal is now the source of two thirds of the exotic species present in the Basin (Galil et al. 2014, 2015, 2017; Fortič et al. 2023).

There are important differences between the Mediterranean and the tropical western Atlantic. The Mediterranean is a temperate/sub-tropical sea dominated by rocky reefs, seagrass meadows and sandy patches (Bussotti and Guidetti 2011; La Mesa et al. 2011; Kleitou et al. 2021). By contrast, the tropical western Atlantic is dominated by coral reefs, similarly to the native range of lionfish (Kulbicki et al. 2012; Côté and Smith 2018). The species composition and biodiversity of the Mediterranean are also profoundly different from those found in tropical seas (Kallianiotis et al. 2000; Brokovich et al. 2006; Albins and Hixon 2008; La Mesa et al. 2011). Both invasive lionfish populations were founded by individuals that went through selection processes that might favour the survival of the resulting invasive populations in suboptimal conditions. Lionfish establishing in the Atlantic survived through the multiple stressors encountered in the aquarium trade (e.g. catching, transportation) and *P. miles*, establishing in the Mediterranean, survived the suboptimal water parameters encountered either in the Suez Canal or in ballast water. It is unknown how strongly these factors selected on invasive lionfish and to what extent the differences between these stressors are affecting the dynamics of the invasions today. Given the invasive potential of *P. miles*, their different origin from that of lionfish in the Atlantic and the different ecology and biodiversity of the temperate/sub-tropical Mediterranean, specific knowledge on this second invasion is needed. This information will be essential to understand and predict the impact of *P. miles* on the Mediterranean and to design rational and effective mitigation strategies. Here, we review the available information on lionfish ecology, we discuss such knowledge in the context of invasion ecology and highlight major knowledge gaps on the Mediterranean invasion that require future investigation. In addition, we offer an update on the distribution of lionfish in the Mediterranean, where *P. miles* are still spreading.

Lionfish in the Mediterranean

The origin and history of the Mediterranean invasion

The first lionfish ever reported in the Mediterranean was caught by a trawler off the coast of Israel in 1991 and identified as *P. miles* (Golani and Sonin 1992). From that moment, no more lionfish were reported until 2012, when two specimens were captured in Lebanon (Bariche et al. 2013). Soon after, lionfish were reported in Turkey, Cyprus, Greece and Italy (Turan et al. 2014; Crocetta et al. 2015; Iglésias and Frotté 2015; Oray et al. 2015; Turan and Öztürk 2015; Azzurro et al. 2017). Lionfish were first considered invasive in the Mediterranean in 2016, when they were reported in large groups and numbers in Cyprus (Kletou et al. 2016). Lionfish have now established and successfully spread through a large part of the eastern Mediterranean (Gökoğlu et al. 2017; Turan et al. 2017; Dimitriadis et al. 2020; Ulman et al. 2020; Vavasis et al. 2020) and continue to expand their range westwards (Azzurro et al. 2017; Phillips and Kotrschal 2021). Today, invasive lionfish populations are confined to the eastern part of the Mediterranean (Dimitriadis et al. 2020; Phillips and Kotrschal 2021), with only sporadic sightings elsewhere. The northernmost report of lionfish is that of a single individual found near the island of Vis, in Croatia (Dragičević et al. 2021) while the westernmost lionfish was also a single individual sighted in the Alboran Sea, Spain (Fortič et al. 2023). Since no established populations are present at these locations, the individuals in Croatia

and Spain may be the result of isolated aquarium releases. The northernmost part of the Aegean Sea has also remained free from lionfish, probably due to the colder waters (Dimitriadis et al. 2020; Phillips and Kotrschal 2021).

Genetic studies revealed that lionfish found in the Mediterranean originate from the Red Sea and that they most likely entered their new range during multiple invasion events through the Suez Canal (Bariche et al. 2017). The origin of Mediterranean lionfish is corroborated by the absence of established populations of *P. volitans* in the Basin; while both *P. miles* and *P. volitans* are often sold together in the aquarium trade (Kimball et al. 2004) and, consequently, are found in the invaded western Atlantic, genetic studies showed that only *P. miles* is present in the Red Sea (Hamner et al. 2007; Kulbicki et al. 2012; Wilcox et al. 2018). Thus, the lionfish population of the Mediterranean is considered the result of *P. miles* entering through the Suez Canal and the reports of *P. volitans* in this sea (e.g. Gürlek et al. (2016); Gökoğlu et al. (2017); Ayas et al. (2018)) are most likely the result of misidentifications or descriptions of individuals that came from isolated aquarium releases.

The northern Red Sea is inhabited by another lionfish species that is biologically and ecologically similar to *P. miles*; *Pterois radiata*. *P. miles* and *P. radiata* often occur together on the coral reefs of the northern Red Sea and in comparable abundances (Gavriel and Belmaker 2021). Interestingly, *P. radiata* has never established in the Mediterranean (Kulbicki et al. 2012; Gavriel and Belmaker 2021). It was hypothesised that *P. radiata* may be less invasive than *P. miles* due to its smaller size and slightly higher degree of habitat and diet specialisation (Kulbicki et al. 2012; Gavriel and Belmaker 2021). Comparative studies analysing behavioural, physiological and reproductive traits in a controlled environment may help elucidate what aspects are preventing *P. radiata* from becoming invasive in the Mediterranean Sea.

Tracking an ongoing invasion

P. miles entered the Mediterranean from one of its easternmost locations and continue to expand westwards and northwards (Bariche et al. 2017; Phillips and Kotrschal 2021), calling for continuous updates to pinpoint the location of their current invasion front. Citizen science, defined as the involvement of lay people in data collection, is an effective tool to track the expansion of invasive species (López-Gómez et al. 2014; Larson et al. 2020; Hermoso et al. 2021). This is especially true for species such as *P. miles*; they are appreciated by divers for their attractive morphology and colouration, increasing the chances of lay people spotting and recognising them. *P. miles* are also difficult to misidentify, especially in the Mediterranean, where closely-related species (i.e. native scorpionfishes) have a markedly different appearance. Finally, the awareness amongst lay people and stakeholders on the invasiveness of lionfish is high (Kleitou et al. 2021), making them attentive and willing to collaborate with scientists. Citizen science is, therefore, particularly suited to monitor the invasive range of lionfish in the Mediterranean, a sea where the diving industry is well established and dive centres are numerous (Phillips and Kotrschal 2021).

As a follow-up to Phillips and Kotrschal (2021), we contacted dive centres on the Mediterranean coast to ask whether they see lionfish during their dives and if they remember the first year that they saw them. We used a list of dive centres on

the Mediterranean coast compiled in 2021 (Phillips and Kotrschal 2021). From this list, we contacted all the dive centres that were still open and reachable via email in April 2023. In most countries, we sent emails in two languages: the first language spoken in the country and English. Translations into local languages were provided by native speakers. We sent emails in two languages to make our survey accessible to those who do not speak English fluently and to foreigners running dive centres in countries of which they do not speak the local language. Dive centres in Egypt, Albania, Montenegro, Malta and Israel were contacted only in English. We sent a reminder to every dive centre that did not respond within a week and we recorded responses for four weeks after the reminder. We used the GPS coordinates of the location of dive centres as an estimation of the point where lionfish are seen as most dives are done in the waters close to a dive centre. Any response that we received in a language different from English were translated through Google translate. When a dive centre reported a range of years as an answer to the date of the first sighting (e.g. 2020–2021), we considered the most recent year in the range as year of first sighting. Data were analysed in R 3.6.2 (R Development Core Team 2019). Maps were produced with the package 'leaflet' (version 2.0.4.1, Cheng et al. (2021)).

Contacting 996 dive centres yielded 326 responses (Fig. 1A). Sightings were reported by 82 dive centres, mostly in the eastern Mediterranean (Fig. 1B). Lionfish were seen by almost every dive centre that responded from Israel, Cyprus, Turkey, Greece and Albania. The lionfish reported at the furthest locations from the Suez Canal were reported in Croatia (42.6513°N, 18.0608°E), Malta (35.9500°N, 14.4063°E) and the Italian islands of Sicily (36.7330°N, 15.1205°E) and Sardinia (40.5699°N, 8.2430°E). When compared with the results by Phillips and Kotrschal (2021) (Fig. 1C), our data show that, in just two years, lionfish have expanded their invasive range in the Mediterranean at two fronts: the northern Aegean Sea and the southern Adriatic Sea. While most of the dive centres reported no lionfish in 2021 in the northern part of the Aegean, they almost all did in 2023; the only two dive centres reporting no lionfish in the northern Aegean were also the ones with the northernmost coordinates. A limited expansion can be seen also in the southern Adriatic, where two dive centres reported lionfish sightings in 2023, while none did in 2021.

The years and locations where lionfish were first seen (Fig. 2) corroborate an expansion of the lionfish invasive range in the Mediterranean. Lionfish were first seen in the northern Aegean, Ionian Sea and southern Adriatic between 2020 and 2022. Individuals in Sicily, Sardinia, Croatia and Malta were also seen only in the most recent year range. This suggests that lionfish found at these locations are probably not just the results of aquarium releases; if that was the case, we could have also expected reports in the past. More likely, these individuals have been transported by strong currents from the eastern Mediterranean, either as larvae or eggs. It is important to note that none of the dive centres reporting lionfish in Malta, Italy and Croatia provided pictures and, therefore, misidentification is still a possibility for these sightings. The dive centres reporting sightings at these locations confirmed that there are no established lionfish populations there.

Our results show that the invasive range of *P. miles* continues to expand rapidly in the Mediterranean. Similar to most coral reef fishes, lionfish eggs hatch into pelagic larvae (Ahrenholz and Morris 2010; Vásquez-Yeomans et al. 2011). Larvae are the life stage with the highest dispersal potential in coral reef fishes (Shanks 2009)

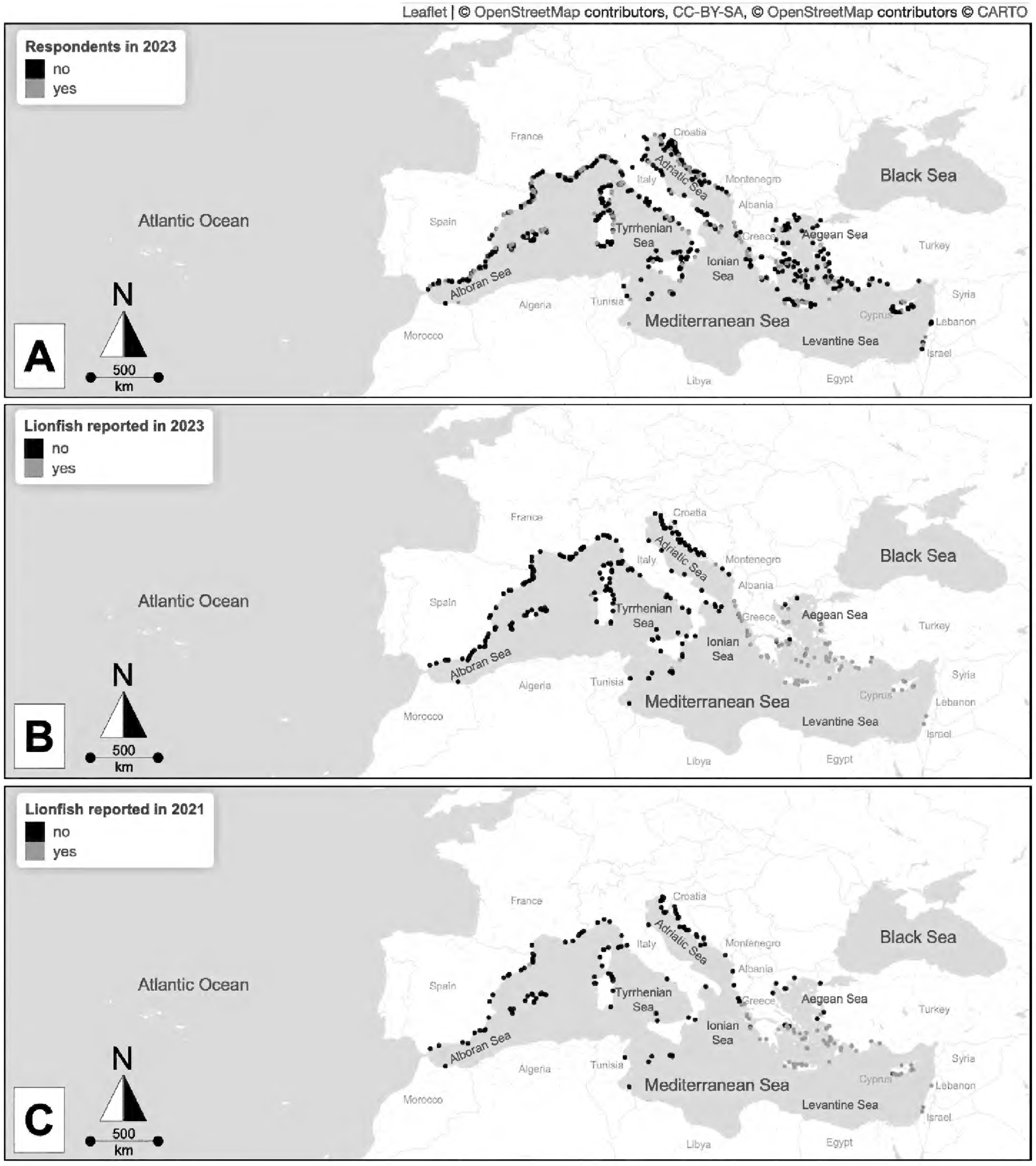

Figure 1. Maps of respondents and lionfish sightings. Panel **A** shows the respondents to our survey in 2023. Each dot represents a dive centre that we contacted, with orange dots representing dive centres that responded and black dots representing dive centres that did not. Panel **B** shows the responses to our survey in 2023. Each dot represents a dive centre that responded to our survey in 2023 with orange dots representing dive centres that reported lionfish sightings and black dots representing dive centres that reported no sightings. Panel **C** shows the responses to the survey in 2021 (Phillips and Kotrschal 2021). Each dot represents a dive centre that responded to the survey in 2021 with orange dots representing dive centres that reported lionfish sightings and black dots representing dive centres that reported no sightings.

and are arguably the main contributor to the dispersal of lionfish, which are highly site-attached as adults (McCallister et al. 2018; Gavriel et al. 2021; Phillips et al. 2024). The Mediterranean invasion is following a similar course to that of other Lessepsian species, which typically expand in the Mediterranean starting from the Levantine Sea and gradually spread westwards and northwards towards the Aegean and Ionian Sea (Azzurro et al. 2013).

Many Lessepsian species remain confined to the eastern Mediterranean and are rarely found in high numbers elsewhere (Azzurro et al. 2013; Galil et al. 2017). A modelling study (Johnston and Purkis 2014) predicted that lionfish were unlikely to become invasive in the Mediterranean. However, our and others' (Azzurro et al. 2017; Phillips and Kotrschal 2021) empirical evidence suggests that the lionfish population of the Mediterranean is well-established and keeps expanding westwards. One of the reasons for the unpredicted success of lionfish could be that their invasion is developing under a strong effect of climate change.

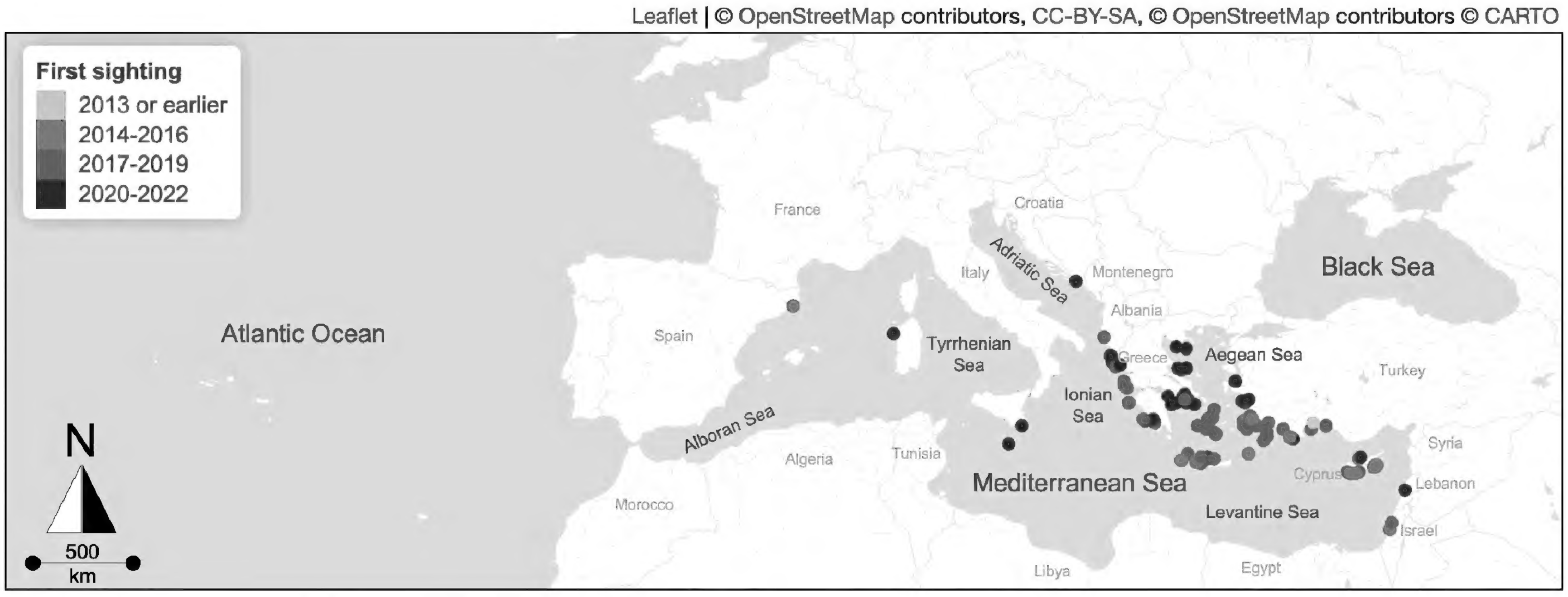

Figure 2. Map of years of first sighting. Each dot represents a dive centre that reported lionfish sightings, either in 2021 or 2023 and included in their response the year when lionfish were first sighted. The darkness of dots shows the year range when lionfish were first sighted.

When climate change is accounted for (Loya-Cancino et al. 2023), lionfish are predicted to find suitable conditions in the Mediterranean. Another reason could be that Johnston and Purkis (2014) considered that lionfish only spread as larvae under the action of natural currents and, because the Mediterranean is less connected by internal currents than the Atlantic, they concluded that lionfish are unlikely to spread across the whole Mediterranean. Although larvae are probably the phase at which lionfish move over long distances, adults can enter new areas as happened recently in Brazil, where lionfish managed to cross the Amazon-Orinoco plume, most likely by adults moving along deeper mesophotic reefs (Soares et al. 2022, 2023). Additionally, the Mediterranean is highly trafficked and this could allow lionfish larvae or eggs to cross large stretches of sea independently from currents if they enter the ballast water. It will be challenging to disentangle the effects of the factors contributing to the unpredicted success of lionfish in the Mediterranean, as multiple phenomena are at play without possibilities to manipulate them.

Remarkably, several *P. miles* sightings were reported in areas that were considered to have winter surface temperatures that are too cold for this species (< 15 °C) such as the northern Aegean and southern Adriatic (Kimball et al. 2004; Johnston and Purkis 2014; Dimitriadis et al. 2020). Although it is too early to conclude that *P. miles* will establish at these locations, climate change has been predicted to facilitate the expansion of tropical invasive species' ranges in the Mediterranean and other ecosystems (D'Amen and Azzurro 2020). Climate change is resulting in a gradual process of 'tropicalisation' of the Mediterranean; the biological community composition is shifting in favour of Lessepsian species at the cost of native ones (Giorgi 2006; Galil et al. 2017). This has already resulted in Lessepsian fishes outweighing and outnumbering native ones in marine protected areas of the eastern Mediterranean (Giakoumi et al. 2019). Another major difference between the Mediterranean and the Red Sea is the stronger seasonality of the former. It remains unknown how the seasonality of Mediterranean waters affects the dynamics and distribution of lionfish and other invasive species of tropical origin.

Our study shows that citizen science is a fruitful approach to monitor lionfish populations at the large scale in the Mediterranean, where the dive industry is strong and awareness towards lionfish is high. Different approaches are needed to monitor the state of the invasion on the southern coasts of the Mediterranean, where data are lacking and the number of dive centres is extremely low (Fig. 1A).

When we contacted members of a Libyan spearfishing association through social media, they reported seeing lionfish relatively frequently on the (eastern) Libyan coast. Moreover, lionfish were reported at several locations on the southern coast of the Mediterranean in the past, including Tunisia (Dailianis et al. 2016; Al Mabruk and Rizgalla 2019). This suggests that, as expected, the lionfish invasion and its expansion are not limited to the northern coast of the Mediterranean.

The evolutionary ecology of invasive lionfish across ranges

Lionfish morphology and habitat use

Lionfish have 18 venomous spines; one on each of the first 13 rays of their dorsal fin, one on each of their pelvic fins and three on their anal fin (Aktaş and Mirasoğlu 2017). They show high site fidelity and often return to the same hiding place over the course of several weeks (McCallister et al. 2018; Gavriel et al. 2021; Phillips et al. 2024), although this can vary significantly at the individual level (Tamburello and Côté 2015; Gavriel et al. 2021). Lionfish are often found, either individually or in small groups, hiding in caves and crevices during the day and swim in the open only at dawn and dusk to hunt for prey (Cure et al. 2012; McCallister et al. 2018; D'Agostino et al. 2020; Gavriel et al. 2021). The eastern Mediterranean offers a markedly different habitat from the coral reefs of the Indo-Pacific and the tropical Atlantic (Kulbicki et al. 2012; Côté and Smith 2018). The Mediterranean is a sub-tropical environment dominated by rocky reefs, seagrass meadows and sandy patches (Bussotti and Guidetti 2011; La Mesa et al. 2011; Kleitou et al. 2021). Despite these habitat differences, *P. miles* have established well in the Mediterranean and have already reached higher population densities than in their native range (Kulbicki et al. 2012; Phillips et al. 2024). It is perhaps not surprising that *P. miles* are thriving in the eastern Mediterranean as, in the western Atlantic, lionfish have been reported in habitats that are novel for this species, including mangrove forests, river estuaries and seagrass beds (Barbour et al. 2010; Jud et al. 2011; Claydon et al. 2012). Analyses of the population structure and dissections of females indicate that the Mediterranean population of *P. miles* is reproducing and will remain a stable presence (Savva et al. 2020; Mouchlianitis et al. 2022).

Predation ecology

Fishes make up most of the lionfish diet (Barbour et al. 2010; Harms-Tuohy et al. 2016; Zannaki et al. 2019), although they have been reported to also feed on invertebrates (Valdez-Moreno et al. 2012). Lionfish are stalking, gape-limited predators: they slowly follow their prey, sometimes for several minutes, with flared pectoral fins before striking and swallowing them whole (Green et al. 2011; Green and Côté 2014). They tend to prefer small, shallow-bodied benthic and demersal fishes in the Caribbean (Green and Côté 2014; Ritger et al. 2020) and show a similar prey preference in the Mediterranean, where they also adopt the same hunting strategy (Zannaki et al. 2019; D'Agostino et al. 2020). In their native range and the invaded Atlantic, lionfish are a widespread component of the community of coral reef predators (Lesser and Slattery 2011; Cure et al. 2012; Kulbicki et al. 2012; Côté and Smith 2018). In the Atlantic, *P. volitans* can have strike success rates as high as 85%, the highest reported in animals in the wild (Vermeij 1982; Green et al. 2011).

The high predation effectiveness in their invaded range has been attributed, at least in part, to prey naïveté (Côté and Smith 2018) (but see Cure et al. (2012)). The 'naïve prey hypothesis' (or 'prey naïveté hypothesis') posits that prey that are exposed to an exotic predator are not prepared to recognise or effectively react to it due to a lack of co-evolutionary history (Sih et al. 2010). Numerous studies support the relevance of prey naïveté in the lionfish invasion in the Atlantic. For instance, several prey species do not react to lionfish with the same readiness as they do with native predators (Anton et al. 2016; McCormick and Allan 2016; Haines and Côté 2019, but see Marsh-Hunkin et al. 2013). In the eastern Mediterranean, exotic prey species from the Red Sea, which co-evolved with *P. miles*, are abundant and occur together with Mediterranean prey. Exotic prey show a markedly higher flight initiation distance when a lionfish is approaching them compared to Mediterranean species, supporting the hypothesis that prey naïveté is also relevant in the Mediterranean invasion (D'Agostino et al. 2020).

Experiments on prey naïveté in the context of lionfish invasions raise the question of whether the selection pressure posed by this new predator will result in adaptations in local prey. It follows from the definition of prey naïveté that it can be counteracted by evolutionary adaptation: after several generations of co-existence with a novel predator, prey should evolve innate responses (Anton et al. 2020). However, how rapidly can such evolutionary adaptations evolve in prey? This is an unresolved question: some estimates based on data on multiple taxa suggest that hundreds of generations are needed (Anton et al. 2020), while there is evidence showing that 10–30 generations can be enough for predators to drive evolutionary changes in prey (O'Steen et al. 2002; Nunes et al. 2014; Melotto et al. 2020). The great variability in the number of generations needed for local prey to evolve an innate response to predators is probably explained by factors such as the pressure posed by predators and the genetic variability of prey populations (Nunes et al. 2014). The potential for prey to adapt to a new predator such as lionfish is of high scientific relevance, but also has practical implications because it will determine the long-term effects on the local prey communities of the Mediterranean and western Atlantic. In an experiment in the western Atlantic (Kindinger 2015), the antipredator response of damselfish (*Stegastes planifrons*) to *P. volitans* was measured and compared to that displayed against a control, native predator. Damselfish were generally naïve to *P. volitans*, including individuals from populations that had co-existed with lionfish for three and seven years (Kindinger 2015). Local adaptation by prey to *P. miles* has never been tested in the Mediterranean.

Prey naïveté interferes with innate predator recognition in animals (Sih et al. 2010; Anton et al. 2020). However, this is not the only mechanism resulting in prey reacting to a predator. Individual fishes can learn which species can pose a threat to their survival through associative learning (Kelley and Magurran 2003). Predator recognition can be learned either directly, when a fish escapes an attack from a predator or indirectly when an individual observes predation events or associates the presence of a predator with the presence of danger-related cues (e.g. blood, stress pheromones) from other fishes (Brown 2003). Learned predator recognition is pervasive in fishes (Brown 2003; Kelley and Magurran 2003; Mitchell et al. 2011); prey fishes can learn to associate danger cues with the presence of a predator during a single conditioning event and retain a behavioural response to that predator for extended periods of time (Chivers and Smith 1994, 1995; Mitchell et al. 2011). Could native prey fishes compensate for their lack of innate

responses to lionfish through learned predator recognition? This is an open question for both the Mediterranean and the Atlantic invasion. Specific work on how well prey species learn that lionfish pose a threat to their survival is limited to one study on a species from the native range of lionfish. This study suggests that even prey that co-evolved with lionfish seem to have difficulties associating them with danger, while other predatory fishes can be learned more readily (McCormick and Allan 2016). This has led to the hypothesis that lionfish circumvent learned predator recognition mechanisms in prey (Côté and Smith 2018). Whether Mediterranean or western Atlantic prey can learn to recognise lionfish as predators is currently unknown and more research is needed to test for the relevance of circumvention of learned predator recognition in lionfish prey.

Predator recognition allows prey to mount an appropriate behavioural response to a predator. Therefore, invasive lionfish are predicted to select on traits that make prey better able to recognise them, either innately or through learning. However, predators can also select on prey behavioural traits that make them less likely to be preyed on due to processes that are not related to predator recognition (Blake and Gabor 2014; Belgrad and Griffen 2016). For example, boldness affects the susceptibility of mud crabs (*Panopeus herbstii*) to be preyed on, creating the potential for predators to select for boldness in this species. Interestingly, boldness has a different effect on susceptibility to predation depending on the predator: toadfish (*Opsanus tau*) consumed more frequently shy mud crabs, while blue crabs (*Callinectes sapidus*) consumed more frequently bold mud crabs (Belgrad and Griffen 2016). This is due to major differences in the hunting strategies of the two predators. In the context of lionfish invasions, individuals of small, benthic fishes that are bolder or simply more active at dusk or dawn can be predicted to be at a higher risk of predation. This is because lionfish hunt at twilight and show a preference for benthic and demersal prey (Cure et al. 2012; Green and Côté 2014; McCallister et al. 2018; D'Agostino et al. 2020; Ritger et al. 2020). We can, therefore, expect lionfish to select for prey individuals whose activity peaks do not coincide with peaks in lionfish hunting and that are, overall, less active or hide more in their hiding spots. This could lead to changes in the behaviour of populations of native fishes in the invasive ranges of lionfish. Whether such selection pressure is at play in the context of lionfish invasions and any consequences on prey populations has never been investigated.

Natural enemies

The 'enemy release hypothesis' posits that exotic organisms benefit from reduced top-down control due to a paucity of natural enemies in their newly-invaded ranges (Colautti et al. 2004). The success of lionfish as invaders has been attributed to a lack of natural predators in the areas that they invade (Côté and Smith 2018). However, the natural enemies and source of mortality of lionfish in their native range remain unknown. It seems unlikely that any predator feeds consistently on the venomous and spinous adult lionfish and events of predation remain sporadic and anecdotal, both in their native and invaded ranges (Côté and Smith 2018). The cornetfish *Fistularia commersonii* and the groupers *Epinephelus striatus* and *Mycteroperca tigris* have been reported to feed on lionfish (Bernadsky and Goulet 1991; Maljković et al. 2008). There is also indication that large groupers may act as biological control agents in the Caribbean (Mumby et al. 2011), although large-scale studies suggest that lionfish density does not correlate with that of groupers

(Hackerott et al. 2013). In the Mediterranean, the only convincing example of predation is that of an octopus (*Octopus vulgaris*) filmed while catching and carrying a lionfish in Cyprus (Crocetta et al. 2021). The scarce knowledge on lionfish predators limits any conclusions on the importance of relaxed predation as an explanation for the high invasiveness of lionfish.

There are other factors than reduced predation on adults that could explain the large population sizes that lionfish reach in their invaded ranges. First, parasites, rather than predators, could be limiting the fitness of adults in their native range (Tuttle et al. 2017). This is supported by data from studies that found relatively low numbers of parasites on invasive lionfish in the Atlantic compared to conspecifics in the native Indo-Pacific (Loerch et al. 2015; Sellers et al. 2015; Tuttle et al. 2017). Such comparisons have not yet included Mediterranean lionfish. Second, a main source of mortality for coral reef fishes is predation at or soon after settlement (Carr and Hixon 1995; Webster 2002; Almany and Webster 2006). Predation on larvae and recruits could, therefore, be the main source of mortality for lionfish (Phillips and Kotrschal 2021). Lionfish larvae are pelagic and probably less defended than the adults (Kitchens et al. 2017) and could be prey of plankton feeders before settlement on the reef and small demersal predators at settlement (Phillips and Kotrschal 2021). Relaxed predation on larvae and recruits could explain the lionfish population increase in their invaded ranges if there were a lower abundance of plankton feeders and predators than in their native range. However, there are no studies comparing the mortality of lionfish recruits between their invasive and native ranges and hypotheses involving lionfish at these stages are difficult to test since spawning in *P. miles* and *P. volitans* has never been described (Côté and Smith 2018).

Impact on invaded ecosystems

The high effectiveness of lionfish as predators implies that they are a potential threat to the native fish community of the areas that they are invading. *P. volitans* are, indeed, having a profound impact on the fish community of the western Atlantic, where they prey heavily on numerous species of very high conservation value (Rocha et al. 2015; Ingeman 2016; Côté and Smith 2018). Invasive *P. volitans* can dramatically reduce the biomass of local species in the Atlantic (Albins and Hixon 2008; Green et al. 2012, 2014), with hypothesised effects on the stability of coral reef ecosystems (Lesser and Slattery 2011). The impact of *P. miles* on the Mediterranean biodiversity has received little consideration. Preliminary assessments suggest that lionfish are reducing the abundance of certain native species and are, therefore, altering the community composition of the Mediterranean (Turan and Doğdu 2022). However, experiments directly linking *P. miles* density with the densities of Mediterranean species are currently lacking.

Interactions with humans and control efforts

The high predation rates shown by lionfish raised concerns on their potential effects on economically valuable species and the fishing industry of the Mediterranean (Kleitou et al. 2019a). It is now well-established that *P. miles* do feed on economically valuable species such as blotched picarels (*Spicara spp.*) and Mediterranean parrotfish (*Sparisoma cretense*) (Zannaki et al. 2019; D'Agostino et al. 2020; Savva et al. 2020). However, specific studies on the impact of lionfish on fisheries are

completely lacking, both in the western Atlantic and Mediterranean. Such studies are difficult to conduct as they necessitate large areas and fish stocks are simultaneously subject to many other stressors such as overfishing, climate change and invasive species other than lionfish (Coll et al. 2010). In addition, the possibility of estimating the impacts of lionfish on Mediterranean fisheries is limited by the lack of knowledge on large-scale effects of *P. miles* on the Mediterranean biodiversity.

Lionfish are venomous and reach large population sizes in their invaded ranges (Kulbicki et al. 2012; Aktaş and Mirasoğlu 2017). Consequently, an additional concern around their invasions is that they could become a danger for bathing tourists and divers (Kosker and Ayas 2022). However, lionfish cannot actively sting; the direction of the spines on the body of a lionfish (bending backwards when the fish is swimming forward) does not allow them to actively attack and sting as wasps or bees do. Therefore, unless they are touched with sufficient pressure, it is unlikely that lionfish spines can penetrate human tissues. Moreover, lionfish tend to move away when a swimmer approaches them closely underwater (Côté et al. 2014). This is probably why only few events of envenomation have been reported in the wild, both in the Mediterranean and western Atlantic. On the other hand, most of the envenomation cases reported in the United States were the result of aquarists manipulating lionfish or doing aquarium maintenance at a close distance from lionfish spines and touched them accidentally (Kosker and Ayas 2022). Similarly, although there is no systematic analysis on lionfish-related accidents in the Mediterranean, most of the cases reported in Cyprus involve people (usually fishermen) directly manipulating lionfish out of the water (Jimenez 2021, personal communication).

Lionfish are highly sedentary and easy to identify by divers due to their conspicuous appearance. This resulted in the involvement of lay people in initiatives aimed at curbing lionfish populations through spearfishing. In so-called ‘culling tournaments’ (or ‘derbies’), divers are encouraged to hunt for lionfish by means of spear-guns (often simpler Hawaiian slings) while free or SCUBA diving (Kleitou et al. 2021). Fishing for lionfish has been incentivised by attempts to create a market for lionfish-derived products such as meat or jewellery (Kleitou et al. 2019b; Simnitt et al. 2020). While jewellery will probably remain a niche product, lionfish meat is appreciated for its taste and increasingly served in local restaurants in the invasive ranges of lionfish (Morris et al. 2011; Simnitt et al. 2020). Culling initiatives were shown to be an effective way of limiting lionfish populations at small scales in the western Atlantic and have the potential to become a management tool with beneficial effects on the conservation of local species (de León et al. 2013; Green et al. 2014; Dahl et al. 2016).

Culling tournaments were organised in the Mediterranean soon after the start of the invasion (Kleitou et al. 2021). Although culling can be effective at the local scale, eradication of lionfish from their invaded ranges is considered impossible for three reasons. First, the effort of having to actively spear-fish for lionfish is high and limits the areas that can be covered in culling tournaments (de León et al. 2013; Malpica-Cruz et al. 2016; Kleitou et al. 2021). Second, culling initiatives are restricted to relatively shallow waters (0–40 m), while invasive lionfish can live in much deeper waters, with large aggregations spotted even beyond 300 m of depth (de León et al. 2013; Nuttall et al. 2014; Gress et al. 2017; Rocha et al. 2018). Third, lionfish adjust to the hunting pressure posed by spear-fishers by becoming more wary towards approaching divers, decreasing the effectiveness of repeated

culling initiatives in the same areas (Côté et al. 2014). Culling should, therefore, be seen as a containment measure, rather than a definitive solution and should be focused on areas of high ecological interest.

Future research avenues

The history and development of the lionfish invasion in the Mediterranean are well-resolved and can be updated promptly through citizen-science initiatives involving the aware and collaborative local dive centres (Phillips and Kotrschal 2021). Our update shows that *P. miles* keep expanding westwards and northwards and are also establishing in waters that were considered too cold for them to live in. Future initiatives should keep monitoring the invasion front as *P. miles* can be expected to continue expanding. Such initiatives should consider approaches that include the southern coast of the Mediterranean. The high awareness of the lay public to the problem of invasive *P. miles* in the Mediterranean resulted in the organisation of successful control initiatives at an early stage of the invasion process (Kleitou et al. 2021). While these initiatives can certainly have beneficial effects at the local scale and contribute to raise awareness towards the major problem of biological invasions, eradication of invasive lionfish is considered impossible.

Studies on the predation ecology of *P. miles* in the Mediterranean remain scant, especially in comparison with the large body of literature available on the Atlantic invasion (Côté and Smith 2018). *P. miles* are thriving in the eastern Mediterranean and are feeding extensively on local fishes of ecological and commercial value (Zannaki et al. 2019; D'Agostino et al. 2020; Savva et al. 2020). However, the community-level impact of *P. miles* on the local biodiversity remains unknown. This is a major knowledge gap for ecologists and policy-makers alike. While assessing the effect of invasive lionfish on the productivity of local fisheries is challenging due to the large scales needed and many confounding factors, it is possible to experimentally measure community-level effects of predation by lionfish (Albins and Hixon 2008; Green et al. 2012, 2014). This could be done through a long-term field experiment monitoring the fish community of the Mediterranean and how it varies depending on the lionfish density and time of invasion. Such experiment would benefit from a manipulative component, where the lionfish density is controlled in experimental patches through culls and the fish community is monitored before and after removals (Albins and Hixon 2008; Green et al. 2012). A control (i.e. unculled patches) can be used to account for natural variation and changes in community composition due to seasonality in the Mediterranean.

Prey naïveté is a contributor to the success of lionfish in the Atlantic and Mediterranean, where native prey show virtually no response to this new predator (Anton et al. 2016; D'Agostino et al. 2020). This raises the question of how long it will take local prey to adapt to this new predator through evolutionary change. Invasive lionfish offer an opportunity to test for local adaptations in marine ecosystems, where adaptations to new predators are particularly understudied (Anton et al. 2020). While the high connectivity of marine systems was traditionally thought to limit the possibilities of local adaptations in marine fishes, increasing evidence is suggesting that local adaptation is widespread in marine systems (Anton et al. 2020). The ongoing Mediterranean invasion offers the potential to work with prey populations that have co-existed with lionfish for different lengths of time. This is because many Mediterranean fishes are distributed across the whole Basin and

lionfish are only present in its eastern part (Phillips and Kotrschal 2021). Individuals from prey populations that co-existed with lionfish for different lengths of time (from 0 to about 10 years) could be studied in a laboratory setting for their reaction towards an approaching lionfish. Individuals from populations that co-existed with lionfish for longer are expected to show stronger behavioural responses to an approaching lionfish. A major limitation is that, because prey can only be wild-caught, it would be impossible to disentangle the relative effects of innate and learned predator recognition in prey reacting to lionfish.

Individual prey fishes have the potential to learn that lionfish are dangerous through associative learning, even in the absence of co-evolutionary history (Brown 2003; Kelley and Magurran 2003). This would give prey an opportunity to rapidly adjust to the presence of a new predator. The only study conducted on learned predator responses to lionfish suggests that it is more difficult for prey to learn that lionfish are dangerous compared to other predators (McCormick and Allan 2016). The alleged ability of lionfish to circumvent learned predator recognition in their prey raises the intriguing question of how they do so. We hypothesise that any difficulty in prey learning that lionfish are dangerous might be linked to their unique morphology. According to the hypothesis of 'prepared fear conditioning', fears are acquired more easily and persist for a longer time if the conditioner is an object that had an impact on the survival of the ancestors of a species (Öhman and Mineka 2001). As lionfish look remarkably different from other fish predators such as snappers, groupers and barracudas (Marshall et al. 2019), prey may be less prepared to associate them with danger. The relevance of this hypothesis in the predation ecology of lionfish could be tested by training naïve (i.e. captive-born) prey to recognise lionfish and other predators as dangerous. This can be done by pairing visual presentations of predators with alarm cues (Brown 2003) and can be followed by similar experiments based on video presentations of real predators and 3D animated models (Johnson and Basolo 2003; Fischer et al. 2014; Scherer et al. 2017; Watve and Taborsky 2019). The use of models shown on screens will allow for changes in the morphology of an approaching lionfish, disentangling which aspects of their morphology and movement contribute the most to their alleged interference with learned predator recognition.

Another major question on the ecology of lionfish, both in their native and invaded ranges, is what their main source of mortality is (Phillips and Kotrschal 2021). This is an important question which could help explain why lionfish reach such high population densities in their invaded ranges. It seems unlikely that any predators feed consistently on adult lionfish because they are well defended by venomous spines and reports of predation events are extremely rare (Côté and Smith 2018). Parasites have been shown to be more abundant on lionfish in their native range compared to the Atlantic, but it is unknown to what extent such parasites exert a control on lionfish population densities (Loerch et al. 2015; Sellers et al. 2015; Tuttle et al. 2017). On the other hand, studies on lionfish parasites in the Mediterranean are entirely lacking. Finally, lionfish could be preyed upon while in their larval or recruit stage, but it is challenging to catch lionfish in high numbers before they are juveniles of a few centimetres in length. This is a critical limitation in the possibilities of directly testing the suitability of lionfish to the diet of plankton feeders (Ahrenholz and Morris 2010; Vásquez-Yeomans et al. 2011). To test any hypotheses on the effects of filter feeders, it would be necessary to have access to lionfish larvae or eggs, which is currently impossible as they have never been ob-

served spawning (Côté and Smith 2018). However, it is possible to investigate the effects of parasites on lionfish with different approaches. A starting point could be a survey on the parasite load of lionfish fished from the Mediterranean Sea. Such data, combined with the available information from other ranges (Loerch et al. 2015; Sellers et al. 2015; Tuttle et al. 2017), would also ensure that any follow-up manipulative experiments are done with realistic parasite loads. Experimental manipulation of parasite load will reveal how parasites impact lionfish behavioural and physiological traits (Timi and Poulin 2020; Hvas and Bui 2022).

Conclusion

While the history and development of the *P. miles* invasion in the Mediterranean are well-resolved and can be easily updated through citizen-science initiatives, the study of the predation ecology of invasive *P. miles* is its infancy, especially at high ecological levels. In addition, the ongoing lionfish invasion in the Mediterranean offers the opportunity to test for major fundamental questions on prey naïveté and learned predator responses. We outlined approaches that could be used to answer these major questions by taking advantage of the ongoing and more recent lionfish invasion in the Mediterranean. Tackling questions such as the community-level impact of lionfish in the Mediterranean and the evolutionary and learned responses in prey will add to the body of knowledge on the best documented invasion in marine ecosystems. This will result in insights into fundamental questions in invasion and predation ecology, but will also be important for policy-makers to estimate the impact of invasive lionfish on human activities.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

D.B. and A.K. conceived the study. D.B. collected the data. D.B. analysed the data and wrote the first version of the manuscript. All authors (D.B., B.A.J.P., R.N., P.A.J., M.N. and A.K.) provided feedback on earlier versions of the manuscript and contributed to its final version.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Ahrenholz DW, Morris Jr JA (2010) Larval duration of the lionfish, *Pterois volitans* along the Bahamian Archipelago. Environmental Biology of Fishes 88(4): 305–309. https://doi.org/10.1007/s10641-010-9647-4

Aktaş Ş, Mirasoğlu B (2017) Lionfish envenomation: Clinical aspect and management. Journal of the Black Sea/Mediterranean Environment 23: 81–87. https://blackmeditjournal.org/volumes-archive/vol23-2017/vol-23-2017-no-1/lionfish-envenomation-clinical-aspect-and-management/

Al Mabruk SAA, Rizgalla J (2019) First record of lionfish (Scorpaenidae: *Pterois*) from Libyan waters. Journal of the Black Sea/Mediterranean Environment 25: 108–114. https://blackmeditjournal.org/volumes-archive/vol-25-2019/vol-25-2019-no-1/first-record-of-lionfish-scorpaenidae-pterois-from-libyan-waters/

Albins M, Hixon M (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. Marine Ecology Progress Series 367: 233–238. https://doi.org/10.3354/meps07620

Almany GR, Webster MS (2006) The predation gauntlet: Early post-settlement mortality in reef fishes. Coral Reefs 25(1): 19–22. https://doi.org/10.1007/s00338-005-0044-y

Anderson CB, Rosemond AD (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. Oecologia 154(1): 141–153. https://doi.org/10.1007/s00442-007-0757-4

Anton A, Cure K, Layman CA, Puntila R, Simpson MS, Bruno JF (2016) Prey naiveté to invasive lionfish *Pterois volitans* on Caribbean coral reefs. Marine Ecology Progress Series 544: 257–269. https://doi.org/10.3354/meps11553

Anton A, Geraldi NR, Ricciardi A, Dick JTA (2020) Global determinants of prey naiveté to exotic predators. Proceedings. Biological Sciences 287(1928): 20192978. https://doi.org/10.1098/rspb.2019.2978

Ayas D, Ağilkaya GŞ, Yağlioğlu D (2018) New record of the red lionfish, *Pterois volitans* (Linnaeus, 1758), in the Northeastern Mediterranean Sea. Düzce University Journal of Science & Technology 6: 871–877. https://doi.org/10.29130/dubited.362703

Azzurro E, Soto S, Garofalo G, Maynou F (2013) *Fistularia commersonii* in the Mediterranean Sea: Invasion history and distribution modeling based on presence-only records. Biological Invasions 15(5): 977–990. https://doi.org/10.1007/s10530-012-0344-4

Azzurro E, Stancanelli B, Di Martino V, Bariche M (2017) Range expansion of the common lionfish *Pterois miles* (Bennett, 1828) in the Mediterranean Sea: An unwanted new guest for Italian waters. BioInvasions Records 6(2): 95–98. https://doi.org/10.3391/bir.2017.6.2.01

Barbour AB, Montgomery ML, Adamson AA, Díaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. Marine Ecology Progress Series 401: 291–294. https://doi.org/10.3354/meps08373

Bariche M, Torres M, Azzurro E (2013) The Presence of the invasive lionfish *Pterois miles* in the Mediterranean Sea. Mediterranean Marine Science 14(2): 292–294. https://doi.org/10.12681/mms.428

Bariche M, Kleitou P, Kalogirou S, Bernardi G (2017) Genetics reveal the identity and origin of the lionfish invasion in the Mediterranean Sea. Scientific Reports 7(1): 6782. https://doi.org/10.1038/s41598-017-07326-1

Belgrad BA, Griffen BD (2016) Predator–prey interactions mediated by prey personality and predator hunting mode. Proceedings of the Royal Society B, Biological Sciences 283(1828): 20160408. https://doi.org/10.1098/rspb.2016.0408

Benkwitt CE (2015) Non-linear effects of invasive lionfish density on native coral-reef fish communities. Biological Invasions 17(5): 1383–1395. https://doi.org/10.1007/s10530-014-0801-3

Bergstrom MA, Mensinger AF (2009) Interspecific resource competition between the invasive round goby and three native species: Logperch, slimy sculpin, and spoonhead sculpin. Transactions of the American Fisheries Society 138(5): 1009–1017. https://doi.org/10.1577/T08-095.1

Bernadsky G, Goulet D (1991) A natural predator of the lionfish, *Pterois miles*. Copeia 1(1): 230–231. https://doi.org/10.2307/1446269

Bianchi CN, Morri C (2000) Marine biodiversity of the Mediterranean Sea: Situation, problems and prospects for future research. Marine Pollution Bulletin 40(5): 367–376. https://doi.org/10.1016/S0025-326X(00)00027-8

Blake CA, Gabor CR (2014) Effect of prey personality depends on predator species. Behavioral Ecology 25(4): 871–877. https://doi.org/10.1093/beheco/aru041

Brokovich E, Baranes A, Goren M (2006) Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. Ecological Indicators 6(3): 494–507. https://doi.org/10.1016/j.ecolind.2005.07.002

Brown GE (2003) Learning about danger: Chemical alarm cues and local risk assessment in prey fishes. Fish and Fisheries 4(3): 227–234. https://doi.org/10.1046/j.1467-2979.2003.00132.x

Bussotti S, Guidetti P (2011) Timing and habitat preferences for settlement of juvenile fishes in the marine protected area of Torre Guaceto (south-eastern Italy, Adriatic Sea). The Italian Journal of Zoology 78(2): 243–254. https://doi.org/10.1080/11250001003774652

Carr MH, Hixon MA (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. Marine Ecology Progress Series 124: 31–42. https://doi.org/10.3354/meps124031

Castellanos-Galindo GA, Robertson DR, Sharpe DMT, Torchin ME (2020) A new wave of marine fish invasions through the Panama and Suez canals. Nature Ecology & Evolution 4(11): 1444–1446. https://doi.org/10.1038/s41559-020-01301-2

Cheng J, Karambelkar B, Xie Y (2021) leaflet: create interactive web maps with the JavaScript 'Leaflet' library. R package version 2.0.4.1. https://CRAN.R-project.org/package=leaflet

Chivers DP, Smith RJF (1994) Fathead minnows, *Pimephales promelas*, acquire predator recognition when alarm substance is associated with the sight of unfamiliar fish. Animal Behaviour 48(3): 597–605. https://doi.org/10.1006/anbe.1994.1279

Chivers DP, Smith RJF (1995) Free-living fathead minnows rapidly learn to recognize pike as predators. Journal of Fish Biology 46(6): 949–954. https://doi.org/10.1111/j.1095-8649.1995.tb01399.x

Claydon JAB, Calosso MC, Traiger SB (2012) Progression of invasive lionfish in seagrass, mangrove and reef habitats. Marine Ecology Progress Series 448: 119–129. https://doi.org/10.3354/meps09534

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7(8): 721–733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

Coll M, Piroddi C, Steenbeek J, Kaschner K, Ben Rais Lasram F, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R, Estrada M, Froglia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos M-S, Koukouras A, Lampadariou N, Laxamana E, López-Fé de la Cuadra CM, Lotze HK, Martin D, Mouillot D, Oro D, Raicevich S, Rius-Barile

J, Saiz-Salinas JI, San Vicente C, Somot S, Templado J, Turon X, Vafidis D, Villanueva R, Voultsiadou E (2010) The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. PLOS ONE 5(8): e11842. https://doi.org/10.1371/journal.pone.0011842

Costello MJ, Dekeyzer S, Galil BS, Hutchings P, Katsanevakis S, Pagad S, Robinson TB, Turon X, Vandepitte L, Vanhoorne B, Verfaille K, Willan RC, Rius M (2021) Introducing the world register of introduced marine species (WRiMS). Management of Biological Invasions 12(4): 792–811. https://doi.org/10.3391/mbi.2021.12.4.02

Côté IM, Smith NS (2018) The lionfish *Pterois* sp. invasion: Has the worst-case scenario come to pass? Journal of Fish Biology 92(3): 660–689. https://doi.org/10.1111/jfb.13544

Côté IM, Darling ES, Malpica-Cruz L, Smith NS, Green SJ, Curtis-Quick J, Layman C (2014) What doesn't kill you makes you wary? Effect of repeated culling on the behaviour of an invasive predator. PLOS ONE 9(4): e94248. https://doi.org/10.1371/journal.pone.0094248

Crocetta F, Agius D, Balistreri P, Bariche M, Bayhan YK, Çakir M, Ciriaco S, Corsini-Foka M, Deidun A, El Zrelli R, Ergüden D, Evans J, Ghelia M, Giavasi M, Kleitou P, Kondylatos G, Lipej L, Mifsud C, Özvarol Y, Pagano A, Portelli P, Poursanidis D, Rabaoui L, Schembri PJ, Taşkin E, Tiralongo F, Zenetos A (2015) New Mediterranean biodiversity records (October 2015). Mediterranean Marine Science 16(3): 682–702. https://doi.org/10.12681/mms.1477

Crocetta F, Shokouros-Oskarsson M, Doumpas N, Giovos I, Kalogirou S, Langeneck J, Tanduo V, Tiralongo F, Virgili R, Kleitou P (2021) Protect the natives to combat the aliens: Could *Octopus vulgaris* Cuvier, 1797 be a natural agent for the control of the lionfish invasion in the Mediterranean Sea? Journal of Marine Science and Engineering 9(3): 308. https://doi.org/10.3390/jmse9030308

Cure K, Benkwitt CE, Kindinger TL, Pickering EA, Pusack TJ, McIlwain JL, Hixon MA (2012) Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. Marine Ecology Progress Series 467: 181–192. https://doi.org/10.3354/meps09942

D'Agostino D, Jimenez C, Reader T, Hadjioannou L, Heyworth S, Aplikioti M, Argyrou M, Feary DA (2020) Behavioural traits and feeding ecology of Mediterranean lionfish and naiveté of native species to lionfish predation. Marine Ecology Progress Series 638: 123–135. https://doi.org/10.3354/meps13256

D'Amen M, Azzurro E (2020) Lessepsian fish invasion in Mediterranean marine protected areas: A risk assessment under climate change scenarios. ICES Journal of Marine Science 77(1): 388–397. https://doi.org/10.1093/icesjms/fsz207

Dahl KA, Patterson III WF, Snyder RA (2016) Experimental assessment of lionfish removals to mitigate reef fish community shifts on northern Gulf of Mexico artificial reefs. Marine Ecology Progress Series 558: 207–221. https://doi.org/10.3354/meps11898

Dailianis T, Akyol O, Babali N, Bariche M, Crocetta F, Gerovasileiou V, Chanem R, Gökoğlu M, Hasiotis T, Izquierdo-Muñoz A, Julian D, Katsanevakis S, Lipej L, Mancini E, Mytilineou CH, Ounifi Ben Amor K, Özgül A, Ragkousis M, Rubio-Portillo E, Servello G, Sini M, Stamouli C, Sterioti A, Teker S, Tiralongo F, Trkov D (2016) New Mediterranean biodiversity records (July 2016). Mediterranean Marine Science 17(2): 608–626. https://doi.org/10.12681/mms.1734

de León R, Vane K, Bertuol P, Chamberland VC, Simal F, Imms E, Vermeij MJA (2013) Effectiveness of lionfish removal efforts in the southern Caribbean. Endangered Species Research 22(2): 175–182. https://doi.org/10.3354/esr00542

Dimitriadis C, Galanidi M, Zenetos A, Corsini-Foka M, Giovos I, Karachle PK, Fournari-Konstantinidoy I, Kytinou E, Issaris Y, Azzurro E, Castriota L, Falautano M, Kalimeris A, Katsanevakis S (2020) Updating the occurrences of *Pterois miles* in the Mediterranean Sea, with considerations on thermal boundaries and future range expansion. Mediterranean Marine Science 21(1): 62–69. https://doi.org/10.12681/mms.21845

Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences of the United States of America 113(40): 11261–11265. https://doi.org/10.1073/pnas.1602480113

Dragičević B, Ugarković P, Krželj M, Zurub D, Dulčić J (2021) New record of *Pterois* cf. *miles* (Actinopterygii: Scorpaeniformes: Scorpaenidae) from the eastern middle Adriatic Sea (Croatian waters): northward expansion. Acta Ichthyologica et Piscatoria 51(4): 379–383. https://doi.org/10.3897/aiep.51.75811

Edelist D, Rilov G, Golani D, Carlton JT, Spanier E (2013) Restructuring the Sea: Profound shifts in the world's most invaded marine ecosystem. Diversity & Distributions 19(1): 69–77. https://doi.org/10.1111/ddi.12002

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics 41(1): 59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650

Fischer S, Taborsky B, Burlaud R, Fernandez AA, Hess S, Oberhummer E, Frommen JG (2014) Animated images as a tool to study visual communication: A case study in a cooperatively breeding cichlid. Behaviour 151(12–13): 1921–1942. https://doi.org/10.1163/1568539X-00003223

Fortič A, Al-Sheikh Rasheed R, Almajid Z, Badreddine A, Báez JC, Belmonte-Gallegos Á, Bettoso N, Borme D, Camisa F, Caracciolo D, Çinar ME, Crocetta F, Ćetković I, Doğan A, Galiya M, García De Los Ríos Y, Los Huertos Á, Grech D, Guallart J, Gündeğer G, Kahrić A, Karachle PK, Kulijer D, Lombarte A, Marković O, Martínez Jiménez E, Okudan ES, Orlando-Bonaca M, Sartoretto S, Spinelli A, Tuney Kizilkaya I, Virgili R (2023) New records of introduced species in the Mediterranean Sea (April 2023). Mediterranean Marine Science 24(1): 182–202. https://doi.org/10.12681/mms.34016

Galil BS, Marchini A, Occhipinti-Ambrogi A, Minchin D, Narščius A, Ojaveer H, Olenin S (2014) International arrivals: Widespread bioinvasions in European Seas. Ethology Ecology and Evolution 26(2–3): 152–171. https://doi.org/10.1080/03949370.2014.897651

Galil BS, Boero F, Campbell ML, Carlton JT, Cook E, Fraschetti S, Gollasch S, Hewitt CL, Jelmert A, Macpherson E, Marchini A, McKenzie C, Minchin D, Occhipinti-Ambrogi A, Ojaveer H, Olenin S, Piraino S, Ruiz GM (2015) 'Double trouble': The expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. Biological Invasions 17(4): 973–976. https://doi.org/10.1007/s10530-014-0778-y

Galil B, Marchini A, Occhipinti-Ambrogi A, Ojaveer H (2017) The enlargement of the Suez Canal-Erythraean introductions and management challenges. Management of Biological Invasions 8(2): 141–152. https://doi.org/10.3391/mbi.2017.8.2.02

Gavriel T, Belmaker J (2021) Little spatial and temporal segregation between coexisting lionfishes (*Pterois miles* and *Pterois radiata*) in the Red Sea. Israel Journal of Ecology and Evolution 67: 51–59. https://doi.org/10.1163/22244662-bja10005

Gavriel T, Pickholtz R, Belmaker J (2021) Large individual-level variability in diel activity and depth use for the common lionfish (*Pterois miles*). Frontiers in Marine Science 8: 790930. https://doi.org/10.3389/fmars.2021.790930

Giakoumi S, Pey A, Di Franco A, Francour P, Kizilkaya Z, Arda Y, Raybaud V, Guidetti P (2019) Exploring the relationships between marine protected areas and invasive fish in the world's most invaded sea. Ecological Applications: A Publication of the Ecological Society of America 29: e01809. https://doi.org/10.1002/eap.1809

Giorgi F (2006) Climate change hot-spots. Geophysical Research Letters 33(8): 2006GL025734. https://doi.org/10.1029/2006GL025734

Gökoğlu M, Teker S, Julian D (2017) Westward extension of the lionfish *Pterois volitans* Linnaeus, 1758 along the Mediterranean Coast of Turkey. Natural and Engineering Sciences 2(2): 67–72. https://doi.org/10.28978/nesciences.329313

Golani D, Sonin O (1992) New records of the Red Sea fishes, *Pterois miles* (Scorpaenidae) and *Pteragogus pelycus* (Labridae) from the eastern Mediterranean Sea. Japanese Journal of Ichthyology 39(2): 167–169. https://doi.org/10.1007/BF02906001

Goodbody-Gringley G, Chequer A, Grincavitch C, Noyes T, Dowell R, Lundberg A, Corbett E, Smith A (2023) Impacts of recurrent culling of invasive lionfish on mesophotic reefs in Bermuda. Coral Reefs 42(2): 443–452. https://doi.org/10.1007/s00338-023-02354-y

Gozlan RE, St-Hilaire S, Feist SW, Martin P, Kent ML (2005) Disease threat to European fish. Nature 435(7045): 1046–1046. https://doi.org/10.1038/4351046a

Green SJ, Côté IM (2014) Trait-based diet selection: prey behaviour and morphology predict vulnerability to predation in reef fish communities. Journal of Animal Ecology 83: 1451–1460. https://doi.org/10.1111/1365-2656.12250

Green SJ, Akins JL, Côté IM (2011) Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. Marine Ecology Progress Series 433: 159–167. https://doi.org/10.3354/meps09208

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLOS ONE 7(3): e32596. https://doi.org/10.1371/journal.pone.0032596

Green SJ, Dulvy NK, Brooks AML, Akins JL, Cooper AB, Miller S, Côté IM (2014) Linking removal targets to the ecological effects of invaders: A predictive model and field test. Ecological Applications 24(6): 1311–1322. https://doi.org/10.1890/13-0979.1

Gress E, Andradi-Brown DA, Woodall L, Schofield PJ, Stanley K, Rogers AD (2017) Lionfish (*Pterois* spp.) invade the upper-bathyal zone in the western Atlantic. PeerJ 5: e3683. https://doi.org/10.7717/peerj.3683

Gürlek M, Ergüden D, Uyan A, Doğdu SA, Yağlıoğlu D, Öztürk B, Turan C (2016) First record red lionfish *Pterois volitans* (Linnaeus, 1785) in the Mediterranean Sea. Natural and Engineering Sciences 1(3): 27–32. https://doi.org/10.28978/nesciences.286308

Hackerott S, Valdivia A, Green S, Côté IM, Cox CE, Akins L, Layman CA, Precht WF, Bruno JF (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean Reefs. PLOS ONE 8(7): e68259. https://doi.org/10.1371/journal.pone.0068259

Haines LJ, Côté IM (2019) Homing decisions reveal lack of risk perception by Caribbean damselfish of invasive lionfish. Biological Invasions 21(5): 1657–1668. https://doi.org/10.1007/s10530-019-01925-x

Hamner RM, Freshwater DW, Whitfield PE (2007) Mitochondrial cytochrome b analysis reveals two invasive lionfish species with strong founder effects in the western Atlantic. Journal of Fish Biology 71(sb): 214–222. https://doi.org/10.1111/j.1095-8649.2007.01575.x

Harms-Tuohy CA, Schizas NV, Appeldoorn RS (2016) Use of DNA metabarcoding for stomach content analysis in the invasive lionfish *Pterois volitans* in Puerto Rico. Marine Ecology Progress Series 558: 181–191. https://doi.org/10.3354/meps11738

Harris HE, Patterson III WF, Ahrens RNM, Allen MS (2019) Detection and removal efficiency of invasive lionfish in the northern Gulf of Mexico. Fisheries Research 213: 22–32. https://doi.org/10.1016/j.fishres.2019.01.002

Harris HE, Fogg AQ, Gittings SR, Ahrens RNM, Allen MS, Patterson WF III (2020) Testing the efficacy of lionfish traps in the northern Gulf of Mexico. PLOS ONE 15(8): e0230985. https://doi.org/10.1371/journal.pone.0230985

Hermoso MI, Martin VY, Gelcich S, Stotz W, Thiel M (2021) Exploring diversity and engagement of divers in citizen science: Insights for marine management and conservation. Marine Policy 124: 104316. https://doi.org/10.1016/j.marpol.2020.104316

Hvas M, Bui S (2022) Energetic costs of ectoparasite infection in Atlantic salmon. The Journal of Experimental Biology 225(1): jeb243300. https://doi.org/10.1242/jeb.243300

Iglésias SP, Frotté L (2015) Alien marine fishes in Cyprus: Update and new records. Aquatic Invasions 10(4): 425–438. https://doi.org/10.3391/ai.2015.10.4.06

Iglesias R, García-Estévez JM, Ayres C, Acuña A, Cordero-Rivera A (2015) First reported outbreak of severe spirorchiidiasis in *Emys orbicularis*, probably resulting from a parasite spillover event. Diseases of Aquatic Organisms 113(1): 75–80. https://doi.org/10.3354/dao02812

Ingeman KE (2016) Lionfish cause increased mortality rates and drive local extirpation of native prey. Marine Ecology Progress Series 558: 235–245. https://doi.org/10.3354/meps11821

Johnson JB, Basolo AL (2003) Predator exposure alters female mate choice in the green swordtail. Behavioral Ecology 14(5): 619–625. https://doi.org/10.1093/beheco/arg046

Johnston MW, Purkis SJ (2014) Are lionfish set for a Mediterranean invasion? Modelling explains why this is unlikely to occur. Marine Pollution Bulletin 88(1–2): 138–147. https://doi.org/10.1016/j.marpolbul.2014.09.013

Jud ZR, Layman CA, Lee JA, Arrington DA (2011) Recent invasion of a Florida (USA) estuarine system by lionfish *Pterois volitans* / *P. miles*. Aquatic Biology 13(1): 21–26. https://doi.org/10.3354/ab00351

Kallianiotis A, Sophronidis K, Vidoris P, Tselepides A (2000) Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): Seasonal variation in species density, biomass and diversity. Progress in Oceanography 46(2–4): 429–455. https://doi.org/10.1016/S0079-6611(00)00028-8

Kelley JL, Magurran AE (2003) Learned predator recognition and antipredator responses in fishes. Fish and Fisheries 4(3): 216–226. https://doi.org/10.1046/j.1467-2979.2003.00126.x

Kimball M, Miller J, Whitfield P, Hare J (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. Marine Ecology Progress Series 283: 269–278. https://doi.org/10.3354/meps283269

Kindinger TL (2015) Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). Environmental Biology of Fishes 98(2): 487–498. https://doi.org/10.1007/s10641-014-0279-y

Kitchens LL, Paris CB, Vaz AC, Ditty JG, Cornic M, Cowan Jr JH, Rooker JR (2017) Occurrence of invasive lionfish (*Pterois volitans*) larvae in the northern Gulf of Mexico: Characterization of dispersal pathways and spawning areas. Biological Invasions 19(7): 1971–1979. https://doi.org/10.1007/s10530-017-1417-1

Kleitou P, Savva I, Kletou D, Hall-Spencer JM, Antoniou C, Christodoulides Y, Chartosia N, Hadjioannou L, Dimitriou AC, Jimenez C, Petrou A, Sfenthourakis S, Rees S (2019a) Invasive lionfish in the Mediterranean: Low public awareness yet high stakeholder concerns. Marine Policy 104: 66–74. https://doi.org/10.1016/j.marpol.2019.02.052

Kleitou P, Hall-Spencer J, Rees S, Sfenthourakis S, Demetriou A, Chartosia N, Jimenez C, Hadjioannou L, Petrou A, Christodoulides Y, Georgiou A, Andreou V, Antoniou C, Savva I, Kletou D (2019b) Tackling the lionfish invasion in the Mediterranean. the EU-LIFE RELIONMED Project: progress and results. Proceedings of the 1st Mediterranean Symposium on the non-indigenous species, Antalya (Turkey), January 2019. University of Plymouth (Plymouth), 65–70. https://pearl.plymouth.ac.uk/handle/10026.1/13288

Kleitou P, Rees S, Cecconi F, Kletou D, Savva I, Cai LL, Hall-Spencer JM (2021) Regular monitoring and targeted removals can control lionfish in Mediterranean marine protected areas. Aquatic Conservation 31(10): 2870–2882. https://doi.org/10.1002/aqc.3669

Kletou D, Hall-Spencer JM, Kleitou P (2016) A lionfish (*Pterois miles*) invasion has begun in the Mediterranean Sea. Marine Biodiversity Records 9(1): 1–7. https://doi.org/10.1186/s41200-016-0065-y

Kosker AR, Ayas D (2022) The new venomous fish in the Mediterranean: the lionfish. Andvanced Underwater Sciences 2: 40–43. https://publish.mersin.edu.tr/index.php/aus/article/view/64

Kulbicki M, Beets J, Chabanet P, Cure K, Darling E, Floeter SR, Galzin R, Green A, Harmelin-Vivien M, Hixon M, Letourneur Y, de Loma TL, McClanahan T, McIlwain J, MouTham G, Myers R,

O'Leary JK, Planes S, Vigliola L, Wantiez L (2012) Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: Implications for the Atlantic invasion. Marine Ecology Progress Series 446: 189–205. https://doi.org/10.3354/meps09442

La Mesa G, Molinari A, Gambaccini S, Tunesi L (2011) Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. Marine Ecology (Berlin) 32(1): 104–114. https://doi.org/10.1111/j.1439-0485.2010.00404.x

Larson ER, Graham BM, Achury R, Coon JJ, Daniels MK, Gambrell DK, Jonasen KL, King GD, LaRacuente N, Perrin-Stowe TIN, Reed EM, Rice CJ, Ruzi SA, Thairu MW, Wilson JC, Suarez AV (2020) From eDNA to citizen science: Emerging tools for the early detection of invasive species. Frontiers in Ecology and the Environment 18(4): 194–202. https://doi.org/10.1002/fee.2162

Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biological Invasions 13(8): 1855–1868. https://doi.org/10.1007/s10530-011-0005-z

Loerch SM, McCammon AM, Sikkel PC (2015) Low susceptibility of invasive Indo-Pacific lionfish *Pterois volitans* to ectoparasitic *Neobenedenia* in the eastern Caribbean. Environmental Biology of Fishes 98(8): 1979–1985. https://doi.org/10.1007/s10641-015-0415-3

López-Gómez MJ, Aguilar-Perera A, Perera-Chan L (2014) Mayan diver-fishers as citizen scientists: Detection and monitoring of the invasive red lionfish in the Parque Nacional Arrecife Alacranes, southern Gulf of Mexico. Biological Invasions 16(7): 1351–1357. https://doi.org/10.1007/s10530-013-0582-0

Loya-Cancino KF, Ángeles-González LE, Yañez-Arenas C, Ibarra-Cerdeña CN, Velázquez-Abunader I, Aguilar-Perera A, Vidal-Martínez VM (2023) Predictions of current and potential global invasion risk in populations of lionfish (*Pterois volitans* and *Pterois miles*) under climate change scenarios. Marine Biology 170(3): 27. https://doi.org/10.1007/s00227-023-04174-8

Maljković A, Van Leeuwen TE, Cove SN (2008) Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. Coral Reefs 27(3): 501–501. https://doi.org/10.1007/s00338-008-0372-9

Malpica-Cruz L, Chaves LCT, Côté IM (2016) Managing marine invasive species through public participation: Lionfish derbies as a case study. Marine Policy 74: 158–164. https://doi.org/10.1016/j.marpol.2016.09.027

Marsh-Hunkin KE, Gochfeld DJ, Slattery M (2013) Antipredator responses to invasive lionfish, *Pterois volitans*: Interspecific differences in cue utilization by two coral reef gobies. Marine Biology 160(4): 1029–1040. https://doi.org/10.1007/s00227-012-2156-6

Marshall NJ, Cortesi F, de Busserolles F, Siebeck UE, Cheney KL (2019) Colours and colour vision in reef fishes: Past, present and future research directions. Journal of Fish Biology 95(1): 5–38. https://doi.org/10.1111/jfb.13849

McCallister M, Renchen J, Binder BM, Acosta A (2018) Diel activity patterns and Movement of invasive lionfish (*Pterois volitans/P. miles*) in the Florida Keys identified using acoustic telemetry. Gulf and Caribbean Research 9: 27–40. https://doi.org/10.18785/gcr.2901.13

McCormick MI, Allan BJM (2016) Lionfish misidentification circumvents an optimized escape response by prey. Conservation Physiology 4(1): cow064. https://doi.org/10.1093/conphys/cow064

Melotto A, Manenti R, Ficetola GF (2020) Rapid adaptation to invasive predators overwhelms natural gradients of intraspecific variation. Nature Communications 11(1): 3608. https://doi.org/10.1038/s41467-020-17406-y

Mitchell MD, McCormick MI, Ferrari MCO, Chivers DP (2011) Coral reef fish rapidly learn to identify multiple unknown predators upon recruitment to the reef. PLOS ONE 6(1): e15764. https://doi.org/10.1371/journal.pone.0015764

Morris JA, Thomas A, Rhyne AL, Breen N, Akins L, Nash B (2011) Nutritional properties of the invasive lionfish: a delicious and nutritious approach for controlling the invasion. Aquaculture, Aquarium, Conservation & Legislation International Journal of the Bioflux Society 4: 21–26. https://docs.rwu.edu/cgi/viewcontent.cgi?referer=&httpsredir=1&article=1142&context=fcas_fp

Mouchlianitis FA, Kalaitzi G, Kleitou P, Savva I, Kletou D, Ganias K (2022) Reproductive dynamics of the invasive lionfish (*Pterois miles*) in the Eastern Mediterranean Sea. Journal of Fish Biology 100(2): 574–581. https://doi.org/10.1111/jfb.14971

Mumby PJ, Harborne AR, Brumbaugh DR (2011) Grouper as a natural biocontrol of invasive lionfish. PLOS ONE 6(6): e21510. https://doi.org/10.1371/journal.pone.0021510

Nunes AL, Orizaola G, Laurila A, Rebelo R (2014) Rapid evolution of constitutive and inducible defenses against an invasive predator. Ecology 95(6): 1520–1530. https://doi.org/10.1890/13-1380.1

Nuttall MF, Johnston MA, Eckert RJ, Embesi JA, Hickerson EL, Schmahl GP (2014) Lionfish (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) records within mesophotic depth ranges on natural banks in the Northwestern Gulf of Mexico. BioInvasions Records 3(2): 111–115. https://doi.org/10.3391/bir.2014.3.2.09

O'Steen S, Cullum AJ, Bennett AF (2002) Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). Evolution 56(4): 776–784. https://doi.org/10.1111/j.0014-3820.2002.tb01388.x

Öhman A, Mineka S (2001) Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. Psychological Review 108(3): 483–522. https://doi.org/10.1037/0033-295X.108.3.483

Oray IK, Sınay E, Saadet Karakulak F, Yıldız T (2015) An expected marine alien fish caught at the coast of Northern Cyprus: *Pterois miles* (Bennett, 1828). Journal of Applied Ichthyology 31(4): 733–735. https://doi.org/10.1111/jai.12857

Phillips EW, Kotrschal A (2021) Where are they now? Tracking the Mediterranean lionfish invasion via local dive centers. Journal of Environmental Management 298: 113354. https://doi.org/10.1016/j.jenvman.2021.113354

Phillips EW, Bottacini D, Schoonhoven ANM, Kamstra YJJ, De Waele H, Jimenez C, Hadjioannou L, Kotrschal A (2024) Limited effects of culling on the behavior of invasive lionfish (*Pterois miles*) in the Mediterranean. Journal of Fish Biology 2024: 1–10. https://doi.org/10.1111/jfb.15686

Polo-Cavia N, López P, Martín J (2010) Competitive interactions during basking between native and invasive freshwater turtle species. Biological Invasions 12(7): 2141–2152. https://doi.org/10.1007/s10530-009-9615-0

Psomadakis PN, Giustino S, Vacchi M (2012) Mediterranean fish biodiversity: An updated inventory with focus on the Ligurian and Tyrrhenian seas. Zootaxa 3263(1): 1–46. https://doi.org/10.11646/zootaxa.3263.1.1

R Development Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Ricciardi A (2013) Invasive species. In: Meyers RA (Ed.) Encyclopedia of sustainability Science and technology. Springer, New York, 161–178. https://doi.org/10.1007/978-1-4614-5755-8_10

Ritger AL, Fountain CT, Bourne K, Martín-Fernández JA, Pierotti MER (2020) Diet choice in a generalist predator, the invasive lionfish (*Pterois volitans/miles*). Journal of Experimental Marine Biology and Ecology 524: 151311. https://doi.org/10.1016/j.jembe.2020.151311

Rocha LA, Rocha CR, Baldwin CC, Weigt LA, McField M (2015) Invasive lionfish preying on critically endangered reef fish. Coral Reefs 34(3): 803–806. https://doi.org/10.1007/s00338-015-1293-z

Rocha LA, Pinheiro HT, Shepherd B, Papastamatiou YP, Luiz OJ, Pyle RL, Bongaerts P (2018) Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. Science 361(6399): 281–284. https://doi.org/10.1126/science.aaq1614

Savva I, Chartosia N, Antoniou C, Kleitou P, Georgiou A, Stern N, Hadjioannou L, Jimenez C, Andreou V, Hall-Spencer JM, Kletou D (2020) They are here to stay: The biology and ecology of

lionfish (*Pterois miles*) in the Mediterranean Sea. Journal of Fish Biology 97(1): 148–162. https://doi.org/10.1111/jfb.14340

Scherer U, Godin JGJ, Schuett W, Tregenza T (2017) Validation of 2D-animated pictures as an investigative tool in the behavioural sciences: A case study with a West African cichlid fish, *Pelvicachromis pulcher*. Ethology 123(8): 560–570. https://doi.org/10.1111/eth.12630

Schofield PJ (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. Aquatic Invasions 4(3): 473–479. https://doi.org/10.3391/ai.2009.4.3.5

Sellers AJ, Ruiz GM, Leung B, Torchin ME (2015) Regional variation in parasite species richness and abundance in the introduced range of the invasive lionfish, *Pterois volitans*. PLOS ONE 10(6): e0131075. https://doi.org/10.1371/journal.pone.0131075

Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. The Biological Bulletin 216(3): 373–385. https://doi.org/10.1086/BBLv216n3p373

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119(4): 610–621. https://doi.org/10.1111/j.1600-0706.2009.18039.x

Simnitt S, House L, Larkin SL, Tookes JS, Yandle T (2020) Using markets to control invasive species: Lionfish in the US Virgin Islands. Marine Resource Economics 35(4): 319–341. https://doi.org/10.1086/710254

Soares MO, Feitosa CV, Garcia TM, Cottens KF, Vinicius B, Paiva SV, de Sousa Duarte O, Gurjão LM, Dayse de Vasconcelos Silva GR, Camargo Maia R, Previatto DM, Carneiro PBM, Cunha E, Amâncio AC, Sampaio CLS, Ferreira CEL, Pereira PHC, Rocha LA, Tavares TCL, Giarrizzo T (2022) Lionfish on the loose: *Pterois* invade shallow habitats in the tropical southwestern Atlantic. Frontiers in Marine Science 9: 956848. https://doi.org/10.3389/fmars.2022.956848

Soares MO, Pereira PHC, Feitosa CV, Maggioni R, Rocha RS, Bezerra LEA, Duarte OS, Paiva SV, Noleto-Filho E, Silva MQM, Csapo-Thomaz M, Garcia TM, Arruda Júnior JPV, Cottens KF, Vinicius B, Araújo R, Eirado CB, do Santos LPS, Guimarães TCS, Targino CH, Amorim-Reis Filho J, Santos WCR dos (2023) Lessons from the invasion front: Integration of research and management of the lionfish invasion in Brazil. Journal of Environmental Management 340: 117954. https://doi.org/10.1016/j.jenvman.2023.117954

Tamburello N, Côté IM (2015) Movement ecology of Indo-Pacific lionfish on Caribbean coral reefs and its implications for invasion dynamics. Biological Invasions 17(6): 1639–1653. https://doi.org/10.1007/s10530-014-0822-y

Timi JT, Poulin R (2020) Why ignoring parasites in fish ecology is a mistake. International Journal for Parasitology 50(10–11): 755–761. https://doi.org/10.1016/j.ijpara.2020.04.007

Turan C, Doğdu SA (2022) Preliminary assessment of invasive lionfish *Pterois miles* using underwater visual census method in the Northeastern Mediterranean. Ribarstvo 80(1): 38–46. https://doi.org/10.2478/cjf-2022-0005

Turan C, Öztürk B (2015) First record of the lionfish *Pterois miles* (Bennett 1828) from the Aegean Sea. Journal of the Black Sea/Mediterranean Environment 21: 334–338. https://blackmeditjournal.org/wp-content/uploads/10.OZTURK_TURAN.pdf

Turan C, Ergüden D, Gürlek M, Yağlioğlu D, Uyan A, Uygur N (2014) First record of the Indo-Pacific lionfish *Pterois miles* (Bennett, 1828) (Osteichthyes: Scorpaenidae) for the Turkish marine waters. Journal of the Black Sea/Mediterranean Environment 20: 158–163. https://dergipark.org.tr/en/pub/jbme/issue/9830/121752

Turan C, Uygur N, İğde M (2017) Lionfishes *Pterois miles* and *Pterois volitans* in the North-eastern Mediterranean Sea: Distribution, habitation, predation and predators. Natural and Engineering Sciences 2(1): 35–43. https://doi.org/10.28978/nesciences.292355

Tuttle LJ, Sikkel PC, Cure K, Hixon MA (2017) Parasite-mediated enemy release and low biotic resistance may facilitate invasion of Atlantic coral reefs by Pacific red lionfish (*Pterois volitans*). Biological Invasions 19(2): 563–575. https://doi.org/10.1007/s10530-016-1342-8

Ulman A, Tunçer S, Kizilkaya IT, Zilifli A, Alford P, Giovos I (2020) The lionfish expansion in the Aegean Sea in Turkey: A looming potential ecological disaster. Regional Studies in Marine Science 36: 101271. https://doi.org/10.1016/j.rsma.2020.101271

Valdez-Moreno M, Quintal-Lizama C, Gómez-Lozano R, del Carmen García-Rivas M (2012) Monitoring an alien invasion: DNA barcoding and the identification of lionfish and their prey on coral reefs of the Mexican Caribbean. PLOS ONE 7(6): e36636. https://doi.org/10.1371/journal.pone.0036636

Vásquez-Yeomans L, Carrillo L, Morales S, Malca E, Morris Jr JA, Schultz T, Lamkin JT (2011) First larval record of *Pterois volitans* (Pisces: Scorpaenidae) collected from the ichthyoplankton in the Atlantic. Biological Invasions 13(12): 2635–2640. https://doi.org/10.1007/s10530-011-9968-z

Vavasis C, Simotas G, Spinos E, Konstantinidis E, Minoudi S, Triantafyllidis A, Perdikaris C (2020) Occurrence of *Pterois miles* in the island of Kefalonia (Greece): The Northernmost dispersal record in the Mediterranean Sea. Thalassas. Thalassas 36(1): 171–175. https://doi.org/10.1007/s41208-019-00175-x

Vermeij GJ (1982) Unsuccessful predation and evolution. American Naturalist 120(6): 701–720. https://doi.org/10.1086/284025

Villamagna AM, Murphy BR (2010) Ecological and socio-economic impacts of invasive water hyacinth (*Eichhornia crassipes*): A review. Freshwater Biology 55(2): 282–298. https://doi.org/10.1111/j.1365-2427.2009.02294.x

Watve M, Taborsky B (2019) Presence of parents during early rearing affects offspring responses towards predators. Animal Behaviour 158: 239–247. https://doi.org/10.1016/j.anbehav.2019.09.012

Webster MS (2002) Role of predators in the early post-settlement demography of coral-reef fishes. Oecologia 131(1): 52–60. https://doi.org/10.1007/s00442-001-0860-x

Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay WR, Ray GC, Hare JA (2002) Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. Marine Ecology Progress Series 235: 289–297. https://doi.org/10.3354/meps235289

Wilcox CL, Motomura H, Matsunuma M, Bowen BW (2018) Phylogeography of lionfishes (*Pterois*) indicate taxonomic over splitting and hybrid origin of the invasive *Pterois volitans*. The Journal of Heredity 109(2): 162–175. https://doi.org/10.1093/jhered/esx056

Witte F, Goldschmidt T, Wanink J, van Oijen M, Goudswaard K, Witte-Maas E, Bouton N (1992) The destruction of an endemic species flock: Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes 34(1): 1–28. https://doi.org/10.1007/BF00004782

Zannaki K, Corsini-Foka M, Kampouris TE, Batjakas IE (2019) First results on the diet of the invasive *Pterois miles* (Actinopterygii: Scorpaeniformes: Scorpaenidae) in the Hellenic waters. Acta Ichthyologica et Piscatoria 49(3): 311–317. https://doi.org/10.3750/AIEP/02616